

ROOT PARASITISM IN *ATKINSONIA LIGUSTRINA* (A. CUNN. EX F. MUELL.)
F. MUELL.

By BARBARA P. MENZIES, Department of Botany, University of Sydney, and H. S. MCKEE,
Joint Plant Physiology Unit, Department of Botany, University of Sydney, and Division
of Food Preservation and Transport, C.S.I.R.O.

(Fourteen Text-figures.)

[Read 29th April, 1959.]

Synopsis.

A brief survey is given of the terrestrial Loranthaceae. The structure of haustoria of *Atkinsonia ligustrina* (A. Cunn. ex F. Muell.) F. Muell. is described and compared with that found in some other phanerogamous root parasites.

INTRODUCTION.

The family Loranthaceae contains several hundred species, nearly all being parasitic shrubs growing on the branches of trees. Terrestrial species include *Nuytsia floribunda* R.Br., the Christmas tree of Western Australia, several South American species of *Gaiadendron* G. Don, *Loranthus terrestris* Hook. f. and *L. ligustrinus* Wall. in India, *L. buchneri* Engl. in Africa and *Atkinsonia ligustrina*, which occurs sporadically on dry rocky ridges in a restricted area of the Blue Mountains of New South Wales. Various authors, including Danser (1933), Moore and Betche (1893), Ruiz (1940) and Skene (1924), state that some or all of these terrestrial species are non-parasitic, though it should be remembered that with the older writers "non-parasitic" may merely mean "non-epiphytic". Hooker (1890) stated that *Loranthus ligustrinus* is "apparently terrestrial, a root parasite?", and referred to *L. terrestris* as follows: "always growing from the ground and hence probably a root parasite. Dr. Thomson and I gathered this plant at seven or eight localities and never found it attached to an aerial tree branch." Welwitsch (Hiern, 1900) found *L. buchneri* "growing parasitically on the roots of a Malvacea (probably a species of *Sida*), though at first sight terrestrial and not parasitical".

Herbert (1919) has shown that *Nuytsia floribunda* is a root parasite, as was indeed conjectured by Harvey in 1854 (Anonymous, 1869). It attacks a wide range of hosts, including both native and introduced species. The question whether the species of *Gaiadendron* are parasitic or not seems to have been little studied. Ruiz (1940) describes *Loranthus luteus*, presumably one of the species now referred to *Gaiadendron*, as a tree ten to twelve yards high, very beautiful on account of its abundance of yellow flowers, and not parasitic. MacBride (1937) cites in this genus two species referred to *Loranthus* by Ruiz and Pavón in 1802, and to *Phrygilanthus* in 1868 by Eichler. These species, *Gaiadendron ellipticum* (Ruiz et Pavón) Baehni ex MacBride and *G. lanceolatum* (Ruiz et Pavón) Baehni ex MacBride, he states to be "as far as is known, parasitic shrubs". *Gaiadendron*, on this interpretation, appears to contain both terrestrial and epiphytic species. One of the former, *G. punctatum* (Ruiz et Pavón) G. Don, described as a tree over 20 m. high, seems to be the largest of the known Loranthaceae. Finally, MacBride (1937) refers, rather cryptically, to *Phrygilanthus eugenioides* (H.B. et K.) Eichler (= *G. eugenioides* G. Don) as "half-parasitic on trees or growing independently". A personal communication from Dr. M. Cárdenas of Cochabamba, Bolivia, mentions this species as growing either in the soil or as a branch parasite.

Amyema scandens (Van Tieghem) Danser seems able to grow independently in the ground for a time before attacking a host plant. A specimen (McKee 2375) of this

species collected in New Caledonia had a stem two cm. in diameter, attached by many haustoria to the trunk of the host (a small tree of *Spermolepis gummifera* Brong. et Gris). Near ground level the parasitic stem became much thinner and separated from the host, entering the soil where it bore what appeared to be a poorly developed root system. The underground parts and the narrow stem immediately above them were dead, though still attached to the living parasitic stem higher up the stem of the host. *Amyema scandens* grows to a large plant climbing to the tops of tall trees, and in such cases may show no indication that it began life in the ground. Similar observations on this species, and on *Amylotheca pyramidata* (Van Tieghem) Danser, have been recorded by other collectors in New Caledonia, e.g. Compton (Rendle, Baker and Moore, 1921: see description of *Loranthus glaucescens* S. Moore, a name treated by Danser (1936) as a synonym of *Amyema scandens*) and Virot (Guillaumin and Virot, 1953; Virot, 1956). It is of interest that these species seem capable of limited independent growth in the soil; they have not been adequately studied, but there is no evidence that they are ever root parasites. Later collectors have confirmed but hardly extended the following notes made by Balansa on the type specimen (Balansa 498) of *Neophytum scandens* Van Tieghem (now *Amyema scandens* (Van Tieghem) Danser), which he collected in New Caledonia in 1869: "pourvue d'une tige ayant ses racines dans le sol même, elle grimpe au sommet des plus grands arbres, en implantant dans leur bois de distance en distance une racine qui égale souvent en grosseur la tige mère."

TAXONOMY AND NOMENCLATURE.

The species which is the subject of this paper has a somewhat involved synonymy. It was discovered by Allan Cunningham in 1817. He named it *Nuytsia ligustrina*, the name being first published by Lindley (1839), who, however, gave no description. The first description was that of Mueller (1861) who retained Cunningham's name, but later (Mueller, 1865), having received fruiting material, removed the species from *Nuytsia* and erected a new genus *Atkinsonia* for it, named after Miss L. Atkinson, who collected extensively in the Blue Mountains. To quote Mueller's own words: ". . . dicavi praeclarae Ludovicae Atkinson, cujus benignitate hanc et multas alias Neo-Cambriae plantas debeo." The genus has had a chequered history. Bentham and Hooker (1883) sank it in *Loranthus*, while Engler (1894) referred the single species to *Gaiadendron*. Later (Engler, 1897), he divided that genus into two sections: *Eugaiadendron*, containing the South American species, and *Atkinsonia* with one Australian species. Finally, Engler and Krause (1935) restored *Atkinsonia* as a separate genus, the distinguishing character being that in *Gaiadendron* the flowers are in racemes of triads and in *Atkinsonia* in simple triads. Two names cited by Jackson (1895), apparently as distinct, may refer to the present species. These are *Loranthus atkinsoniae* Benth. and *L. epigaeus* F. Muell. Mueller (1865) cites the latter as a synonym, but seems not to have published it; Danser (1933) cites it as *L. epigaeus* Jacks. The specific name *ligustrinus* is preoccupied in *Loranthus* by *L. ligustrinus* Wall., an Indian species. The present species is figured (as *L. atkinsoniae* Benth.) by Oliver (1880) and by Blakely (1922, Plate XXVIII). The only previously published investigation of its parasitism, except for a preliminary note (McKee, 1952) by one of the present authors, appears to be due to Blakely (1922), who examined the roots of several plants without finding haustoria.

DISTRIBUTION AND HOST RANGE.

The species is known only from the Blue Mountains of New South Wales, where it occurs sporadically, often on dry rocky ridges. It is not common, but is usually found in groups of from two to twenty plants. A suggestion that it occurs outside the Blue Mountains comes from Mueller (1860), who states that it "occurs in the Blue Mountains and is said to be found also on the north-eastern tributaries of the Darling". This suggests a northwards extension of the range of the species, but the phrase used is rather vague, as some of the headwaters of the Macquarie, which could be considered a "north-eastern tributary of the Darling", rise in the Blue Mountains, while other rivers

rising as far north as the Carnarvon Ranges in Queensland flow, occasionally at least, to the Darling. Specimens in the National Herbarium, Sydney, all come from the comparatively small area bounded by Linden, Mount Victoria and Mount Wilson, with one outlying locality at Marrangaroo. Material used in the present study came from Woodford and Linden.

A. ligustrina has been reported (McKee, 1952) to form haustoria on the roots of several hosts, including *Acacia intertexta* Sieb., *Platysace linearifolia* (Cav.) Norman (syn. *Trachymene linearis* Spreng.) and the narrow-leaved form of *Leptospermum attenuatum* Sm. Haustoria have also been observed on the roots of *Monotoca scoparia*

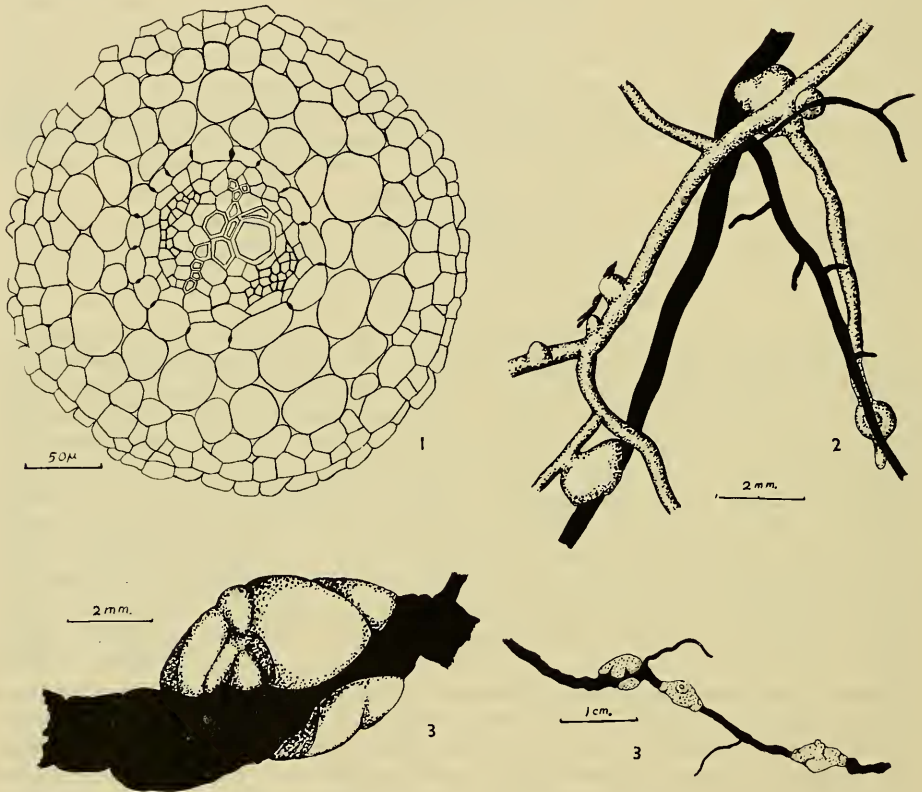


Fig. 1.—Cross-section of a root of *Atkinsonia*.

Fig. 2.—Young roots of *Atkinsonia* (stippled) showing branching and haustoria attacking the host (solid black).

Fig. 3.—An haustorium almost completely surrounding the host root.

R.Br. and *Caustis* sp. The haustoria examined in the present work were growing on the roots of *Acacia intertexta*, *Leptospermum attenuatum* and *Dillwynia ericifolia* Sm. No pronounced differences in behaviour were observed between haustoria on any of these hosts.

ROOT SYSTEM AND HAUSTORIA.

The late Dr. J. McLuckie made preliminary studies on the root system and haustoria of *A. ligustrina*, and raised seedlings which made considerable development in the absence of host plants. His seedlings, preparations and notes were unfortunately lost after his death in 1956. Seedlings were not studied during the present investigation, since a bush fire destroyed the above-ground parts of the plants from which our material was taken. The plants have since developed new shoots, but it will be some

time before they fruit again. For this reason the following account deals only with the root system and haustoria of established plants.

A. ligustrina is a shrub with a large number of leading shoots, growing to a height of about one metre. The root system is entirely subterranean, consisting of five or six fleshy primary roots which rapidly turn blue when damaged. Lateral roots, bearing the haustoria, are freely produced but short-lived. Thus the older primary roots are almost unbranched and bear numerous scars of fallen laterals. Young lateral roots are entirely devoid of root hairs, though Blakely (1922) recorded the presence of numerous root hairs on lateral roots of seedlings.

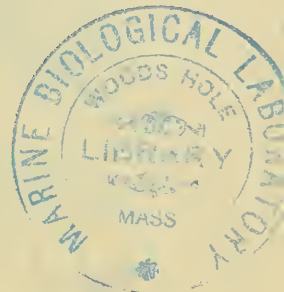
Internally, the structure of the root is comparable with that of other dicotyledons. The apical meristem consists of a small group of cells giving rise to the root tissue and also to a small root cap of about three rows of cells. Differentiation of vascular



Fig. 4.—Cross-section through union of haustorium (stippled) and host (*Leptospermum*). The solid black represents vascular tissue of the haustorium and the broken lines, zones of collapsed cells.

tissue tends to occur early, often less than 100μ from the tip. The mature root is diarch with a well-developed endodermis with distinct casparian bands (Fig. 1). Secondary growth takes place in the normal manner. Periderm is superficial and limited in extent. Branch roots arise in the usual endogenous manner in the pericycle opposite a protoxylem group.

Haustroria arise exogenously in the cortex of the root, their position being unrelated to the orientation of the parent root. They arise near the root tip, but their position is always lateral. They occur singly or in groups. It is possible that their development requires an external stimulus, perhaps proximity to a host root, but without seedlings this could not be investigated. The haustoria are often irregular in shape and may grow out some little distance before reaching a host root. The decayed remains of



numbers of young haustoria were found: these had presumably failed to make contact with a host.

When the host is reached, the haustorium flattens into a disc which attaches itself to the root (Fig. 2). This disc extends more or less evenly in all directions, wrapping itself round the host (Fig. 3). The disc may completely surround a small root, its originally separate parts joining with scarcely any line of division.

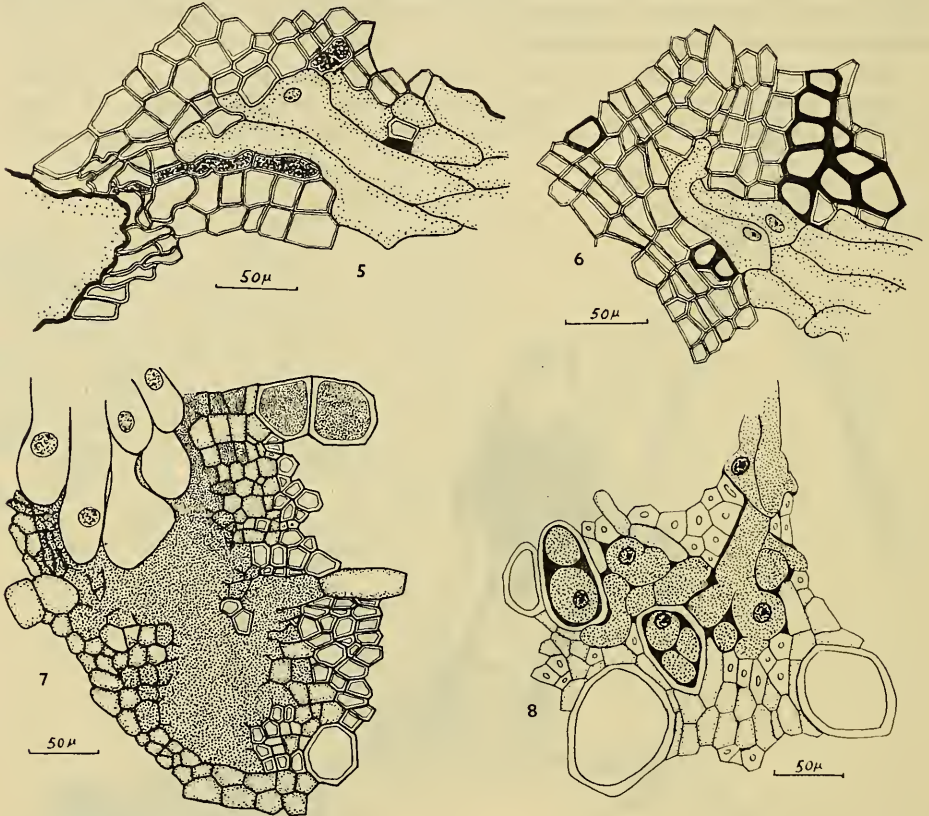


Fig. 5.—Cross-section of parasite union showing elongated cells of the haustorium (stippled) forcing apart the cells of the host xylem. The way in which the parenchyma ray cells have been pushed apart is particularly well shown. (Host *Acacia*.)

Fig. 6.—Cross-section of union of parasite and host, showing the elongated cells at the margin of the haustorium (stippled) which have forced apart the xylem cells of the host (*Acacia*).

Fig. 7.—Cross-section of part of an haustorium (cells left empty) growing through the region of the cambium of the host. In advance of the haustorium is a mass of yellowish material (dense stippling), and some of the same material can be seen in the vessels in the adjacent xylem. Many partly dissolved cells can be seen in the cambial region. (Host *Dillwynia*.)

Fig. 8.—Cross-section of host xylem and haustorium (stippled). In this older union the elongated cells at the margin of the haustorium are surrounded by yellowish material (shown black). Some elongated cells have entered the vessels of the host and grown along with them.

The disc at this stage has a central axis of meristematic tissue surrounded by vacuolated parenchyma. The cells on the attaching surface are elongated with dense contents and large nuclei. At an early stage a zone of collapsed cells appears, extending from the axis to the edges of the disc. Similar zones are found in the haustoria of other semi-parasites.

An outgrowth from the middle of the attached surface of the disc penetrates the host, partly dissolving, but chiefly forcing its way through the epidermis or cork into the cortex. Subsequent behaviour of the haustorium depends on the size of the host root. On a small root it may grow straight into the xylem, sometimes splitting the cylinder open. In a larger root, it may first extend tangentially in the host cortex, disrupting it to such an extent that groups of cortical cells may become embedded in the haustorial tissue. This process of radial growth and lateral expansion may be repeated in cortex, phloem, cambium and finally xylem, so that a complicated system of overlying discs on a central shaft is produced (Fig. 4). Finally the haustorium may grow radially right through the middle of the xylem cylinder.

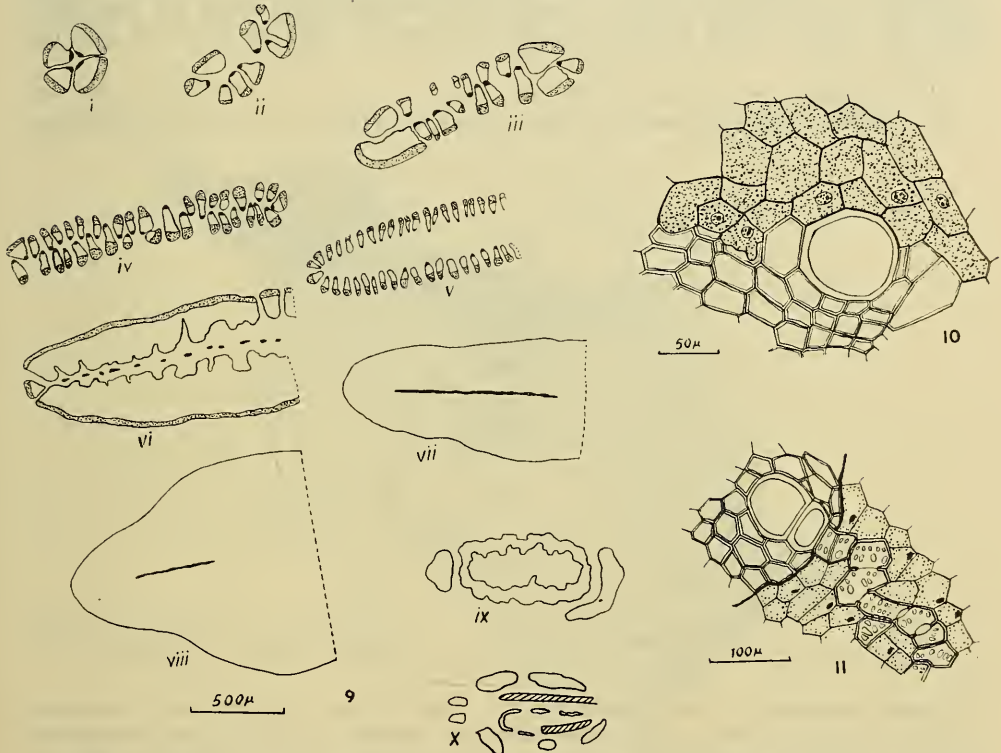


Fig. 9.—I-X. Cross-sections cut at successive levels in the haustorium to show the changes in orientation of the vascular tissue. See text for details. Phloem stippled, xylem clear, host xylem cross-hatched.

Fig. 10.—Xylem union between host and haustorium: young stage in which cells of the haustorium (stippled) are closely adpressed to the vessels of the host. (Host *Acacia*.)

Fig. 11.—Xylem union between host and haustorium: older stage in which the haustorial cell in contact with the host vessel has been differentiated into a xylem vessel segment which links up with the main vascular tissue of the haustorium. (Host *Acacia*.)

The advancing edges both of disc and shaft of the haustorium are composed of greatly elongated cells which have dense contents and large nuclei (Figs. 5, 6) and seem to force the opposing tissue apart. The cells are, nevertheless, quite plastic and in the xylem fit neatly into the gaps they have made (Fig. 5). In the phloem or cortex the cells reach their greatest size and are often embedded in masses of gummy material (Fig. 7). A similar gummy material is found in host xylem vessels near haustoria. It may result from a wound reaction by the host, or from the dissolving of host cells by the haustorium. Elongated haustorial cells sometimes grow inside vessels of the host. The margin of the haustorium is composed of glandular cells smaller than those just described, but also probably able to dissolve host tissue (Fig. 8).

The development of the vascular system of the haustorium begins near the parent root with two or four groups of xylem, each with an associated phloem group (Fig. 9). Within a few millimetres these groups break up to form a small irregular ring of open, collateral bundles as in *Dendrophthoë falcata* (Singh, 1954) and *Loranthus micranthus* (Menzies, 1954). At first the bundles tend to lie side by side with the relative positions of the xylem and phloem alternating in alternate bundles. Then the number of bundles increases and they become arranged in an ellipse. Further down (but still outside the host) the proportion of vascular tissue increases, the xylem consisting of a solid, somewhat squashed cylinder of cubical, reticulate vessels surrounded by what appears to be precambial or cambial tissue which differentiates into more xylem. No phloem was recognized at this level or below. Sections of the haustorium within the host plant show the xylem cylinder breaking up into a number of branches going out into the haustorial discs.

Connections between xylem of host and parasite are easily found round the margins of the haustoria inside the xylem. In early stages a meristematic cell of the haustorium

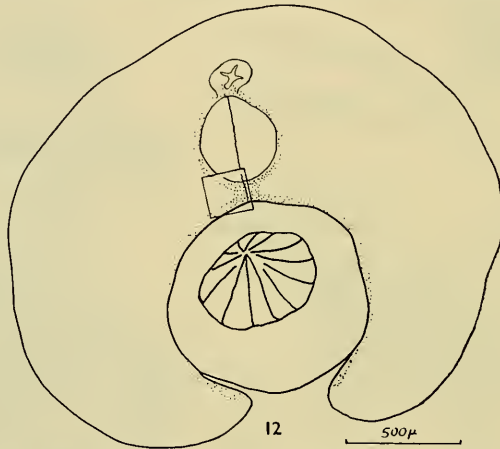


Fig. 12.—Section through host and parasite. No penetration of the host has yet taken place and a "gland" is a conspicuous feature of the haustorium. (Host *Leptospermum*.)

is closely appressed to a host vessel (Fig. 10). This cell later matures into a reticulate or pitted vessel which is continuous with the vascular system of the haustorium (Fig. 11). Zones of collapsed cells occur in all parts of the haustorium, but the conspicuous zones found round each xylem connection in *Loranthus micranthus* are absent in *Atkinsonia*.

The life of an haustorium appears to be relatively short. The haustoria found varied from a millimetre to a centimetre in diameter, but this variation appears to be related to size of root attacked rather than to age. They were all yellowish in colour and in all the vascular tissue had developed to approximately the same extent. Large woody haustoria with considerable secondary thickening, such as one sees in *Loranthus*, were not found. It seems probable that lateral roots and haustoria last only about a year and are then replaced by new ones.

HAUSTORIAL "GLANDS".

In *Santalum album*, *Cansjera rheedii* and *Olax scandens* (Barber, 1906) and also possibly in *Thesium* (Solms-Laubach, 1867-8), the haustorium appears to contain a "gland" secreting enzymes which function in the penetration of the host. A very similar structure has been found in the haustorium of *Atkinsonia*. The shape of this "gland" is shown in Figure 12. It first appears as two rows of elongated meristematic cells, those of one row abutting closely onto those of the other. As the "gland" becomes

older these cells become longer and longer and their contents begin to withdraw from contiguous walls. This continues until the "gland" consists of two rows of empty elongate cells surrounded by a very small-celled meristematic tissue (Fig. 13). Finally the elongated cells disappear altogether, leaving a cavity filled with red-staining amorphous material and fragments of cell and other débris. In *Atkinsonia* such "glands" were found only in haustorial discs which had not penetrated the host, but they were not found in all discs prior to penetration. No "glands" were found in older haustoria which had entered the host, nor was there any trace that a "gland" had ever been present. The "glands" appear to occupy the position taken up by the procambial tissue in haustoria which have penetrated the host. The orientation of the haustorial tissues round the "gland" also suggests that it is an abnormality following failure to penetrate the host rather than a transient feature of the normally developing haustorium. A possible sequence of events is that the penetration process grows out

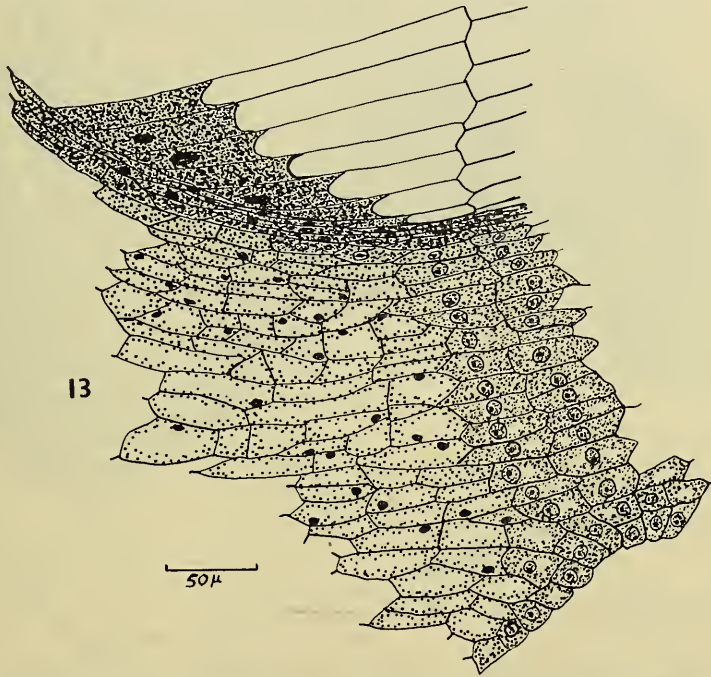


Fig. 13.—Detail of portion of Fig. 12 in the region of the "gland". The contents of the cells of the "gland" have contracted considerably. The tissues round the "gland" have dense contents and appear to have been considerably compressed. The density of the stippling indicates the density of the cell contents.

from the middle of the attachment disc, but, unable for some reason to penetrate the host, is forced back into the attachment disc and its elongated cells begin to digest one another. This would account for the pieces of débris, apparently not belonging to the haustorium itself, which are found within old "glands".

The structures figured by Barber (1906) for *Santalum album* show many similarities with those described above. Most of the "glands" he illustrates are in haustoria which have made little or no penetration, and he notes that the presence of a "gland" before penetration is not invariable. The peculiar structure he interprets as the "opening-up" of a "gland" would be more easily understood as a stage in "gland" formation on our interpretation. A similar example in a young haustorium of *Atkinsonia* has been found (Fig. 14): this could only be interpreted as the closing-up of a developing "gland". A difficulty encountered both with *Santalum* and *Atkinsonia* is that very few stages are found in which the haustorium is in the act of passing

through the cortex. This must be due to the fact that this stage is passed through very quickly.

McLuckie studied the haustoria of *Olax stricta* R.Br., a brief summary of his results being given by McLuckie and McKee (1954), and some observations on the same species were made in connection with the present work. *Olax* also shows a haustorial gland somewhat resembling those found in *Atkinsonia* and *Santalum*. Further investigation on a wider range of material is desirable to permit detailed comparison of the structures in *Olax* with those of the other two genera.

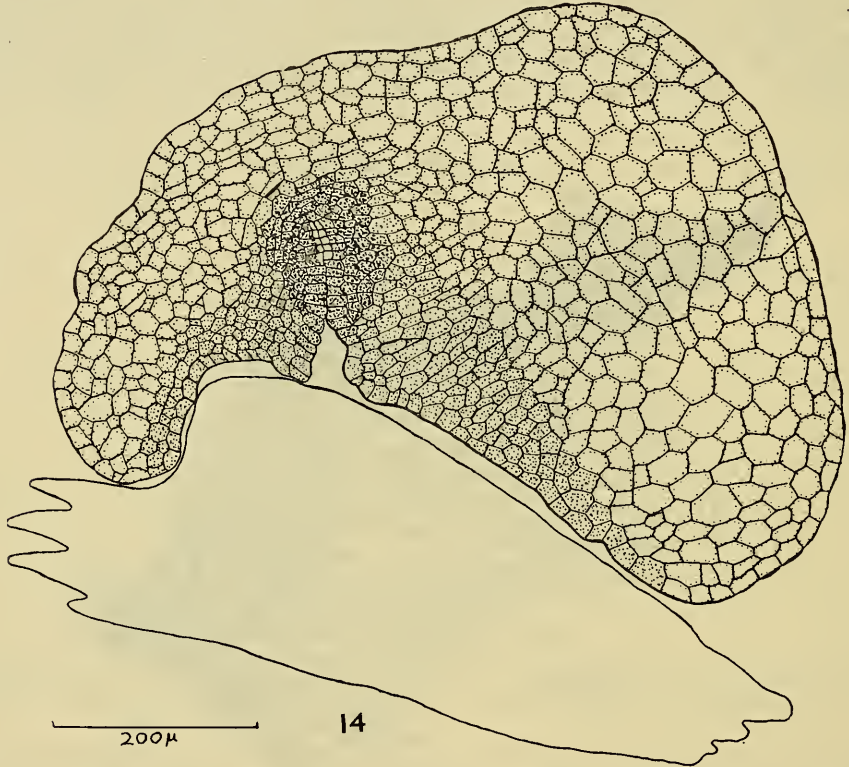


Fig. 14.—Young haustorium (stippled) in contact with the host.

No reference has been found to a "gland" of this type in aerial members of the Loranthaceae. It is interesting that a structure found in two families of root parasites should occur also in a root parasite belonging to a family composed predominantly of branch parasites.

Acknowledgements.

The authors wish to thank Miss I. Bowden, Woodford, N.S.W., for indicating the position of the plants which provided most of the material studied; the late Dr. J. McLuckie for encouragement and co-operation in the early stages of the work; and the following for helpful correspondence or discussion: Dr. S. T. Blake (Brisbane), Dr. M. Cárdenas (Cochabama, Bolivia), Prof. A. Guillaumin (Paris), Mr. L. A. S. Johnson (Sydney), Prof. D. Thoday (Bangor), Dr. R. Virot (Paris).

References.

- ANONYMOUS, 1869.—*Memoir of W. H. Harvey, M.D., F.R.S. Bell and Daldy*, London.
 BENTHAM, G., and HOOKER, J. D., 1883.—*Genera Plantarum*, 3: 212. Reeve, London.
 BARBER, C. A., 1906.—Studies in root-parasitism. The haustorium of *Santalum alum*. 1. Early stages, up to penetration. *Mem. Dep. Agric. in India*, I (1): 1-30.

- BLAKELY, W. F., 1922.—The Loranthaceae of Australia, Part ii. *Proc. Linn. Soc. N.S.W.*, 47: 199-222.
- DANSER, B. H., 1933.—A new system for the genera of Loranthaceae Loranthoideae, with a nomenclator for the Old World species of this subfamily. *Verh. Akad. Wet. Amst.* 2 Sect., 29: 17.
- DANSER, B. H., 1936.—The Loranthaceae Loranthoideae of the tropical archipelagos east of the Philippines, New Guinea and Australia. *Bull. Jard. Bot. Buitenzorg* 3 Sér., 14, 73-98.
- ENCLER, A., 1894.—Loranthaceae. In: *Die Natürlichen Pflanzenfamilien*. Auf. I, 3(1): 156-198. *Wilhelm Engelmann*, Leipzig.
- ENGLER, A., 1897.—*Nachtrag zum II-IV Teil Pflanzenfamilien*. *Wilhelm Engelmann*, Leipzig.
- ENGLER, A., and KRAUSE, K., 1935.—Loranthaceae. In: *Die Natürlichen Pflanzenfamilien*. Auf. 2, 16b: 98-203. *Wilhelm Engelmann*, Leipzig.
- GUILLAUMIN, A., and VIROT, R., 1953.—Contribution à la flore de la Nouvelle-Calédonie, (CII). Plantes récoltées par M. R. Virot. *Mém. Mus. Nat. Hist. Nat.* (Paris). Nouvelle Série. Série B, Botanique, IV, fasc. 1, 1-82.
- HERBERT, D. A., 1918-19.—The Western Australian Christmas tree, *Nuytsia floribunda*, its structure and parasitism. *J. and Proc. Roy. Soc. W. Aust.*, 5: 72-88.
- HIERN, W. P., 1900.—*Catalogue of the African plants collected by Dr. Friederich Welwitsch in 1853-61, Dicots*. Part IV. *British Museum (Natural History)*, London.
- HOOKER, J. D., 1890.—*Flora of British India*. Vol. 5: 207-8.
- JACKSON, B. D., 1895.—*Index Kewensis*, 2: 320. *University Press*, Oxford.
- LINDLEY, J., 1839.—Sketch of the vegetation of the Swan River Colony. Appendix to the index to the first 23 volumes of Edward's Botanical Register, London.
- MACBRIDE, J. F., 1937.—*Flora of Peru*. Vol. XIII, Part 2, No. 2, *Field Museum of Natural History*, Chicago.
- MCKEE, H. S., 1952.—Root parasites in Loranthaceae. *Nature*, Lond., 170: 40.
- MCLUCKIE, J., and MCKEE, H. S., 1954.—*Australian and New Zealand Botany*. *Associated General Publications*, Sydney.
- MENZIES, B. P., 1954.—Seedling development and haustorial system of *Loranthus micranthus* Hook. f. *Phytomorphology*, 4: 397-409.
- MOORE, C., and BETCHE, E., 1893.—*Handbook of the Flora of New South Wales*. *Government Printer*, Sydney.
- MUELLER, F. VON, 1860.—*Essay on the plants collected by Mr. Eugene Fitzalan during Lieut. Smith's expedition to the estuary of the Burdekin by Dr. Ferdinand Mueller*, *Government Botanist for the colony of Victoria*. Melbourne.
- MUELLER, F. VON, 1861.—*Fragm.*, 2: 130.
- MUELLER, F. VON, 1865.—*Fragm.*, 5: 34.
- OLIVER, D., 1880.—*Hooker's Icones Plantarum*. 3rd series, Vol. 4, Plate 1319.
- RENDLE, A. B., BAKER, E. G., and MOORE, S. LE M., 1921.—A systematic account of the plants collected in New Caledonia and the Isle of Pines by Prof. R. H. Compton, M.A., in 1914. Part I. Flowering Plants (Angiosperms). *J. Linn. Soc. (Bot.)*, 45: 245-417.
- RUIZ, H., 1940.—*Travels of Ruiz, Pavón and Dombey in Peru and Chile (1777-1778)*. Translated by B. E. Dahlgren. *Field Museum of Natural History*, Chicago.
- SINGH, B., 1954.—Studies in the family Loranthaceae—list of new hosts of *Dendrophthoe falcata* (L.f.) Ettings., its relations with hosts, the anatomy of its seedlings and mature haustorium. *Agra Univ. J. Res.*, 3: 301-315.
- SKENE, M., 1924.—*Biology of Flowering Plants*. *Sedgwick and Jackson*, London.
- SOLMS-LAUBACH, H. CRAF ZU, 1867-1868.—Über den Bau und die Entwicklung der Ernährungsorgane parasitischer Phanerogamen. *Pringsheim's Jb. wiss. Bot.*, 6: 539-560.
- VIROT, R., 1956.—*La végétation canaque*. Thèse, Faculté des Sciences de l'Université de Paris.